

Variation in phenology and density differentially affects predator–prey interactions between salamanders

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Abstract Variation in the timing of breeding (i.e., phenological variation) can affect species interactions and community structure, in part by shifting body size differences between species. Body size differences can be further altered by density-dependent competition, though synergistic effects of density and phenology on species interactions are rarely evaluated. We tested how field-realistic variation in phenology and density affected ringed salamander (*Ambystoma annulatum*) predation on spotted salamanders (*Ambystoma maculatum*), and whether these altered salamander dynamics resulted in trophic cascades. In outdoor mesocosms, we experimentally manipulated ringed salamander density (low/high) and breeding phenology (early/late) of both species. Ringed salamander body size at metamorphosis, development, and growth were reduced at higher densities, while delayed phenology increased hatchling size and larval development, but reduced relative growth rates. Survival of ringed salamanders was affected by the interactive effects of phenology and density. In contrast, spotted salamander growth, size at metamorphosis, and survival, as well as the biomass of lower trophic levels, were negatively affected primarily by ringed salamander density. In an additional mesocosm

experiment, we isolated whether ringed salamanders could deplete shared resources prior to their interactions with spotted salamanders, but instead found direct interactions (e.g., predation) were the more likely mechanism by which ringed salamanders limited spotted salamanders. Overall, our results indicate the effects of phenological variability on fitness-related traits can be modified or superseded by differences in density dependence. Identifying such context dependencies will lead to greater insight into when phenological variation will likely alter species interactions.

Keywords *Ambystoma* · Competition · Intraguild predation · Phenological shift · Priority effects

Introduction

Variation in the timing of life history events, or phenology, can substantially impact the dynamics of both populations and communities (Forrest and Miller-Rushing 2010; Miller-Rushing et al. 2010). Such variation is especially important for species interactions, as it can dictate whether certain life stages appear when required resources are available (Durant et al. 2007; McKinney et al. 2012), with even subtle changes to the timing of overlap leading to altered population trajectories (Revilla et al. 2014). Phenological variation can also shift the timing of when different species meet during their respective ontogenies, which can alter the strength of their interactions (Yang and Rudolf 2010). Altered interactions stemming from variation in phenology can even change dynamics across multiple trophic levels (Both et al. 2009). The ultimate consequences of phenological variation include the decoupling of species interactions, match–mismatch scenarios, and the development of novel communities (Durant et al. 2007; Urban et al. 2012; Revilla et al. 2014).

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However, investigations addressing phenological variability have only recently been identified as an essential but often missing component in species interactions and community ecology (Miller-Rushing et al. 2010; Yang and Rudolf 2010; Nakazawa and Doi 2012). A better understanding of such processes is especially important, as climate-induced shifts in phenology have been documented in a growing number of taxa (Parmesan and Yohe 2003; Visser and Both 2005; Parmesan 2006).

While documenting variation in phenology of natural populations is a first step in understanding their importance to food web interactions, the underlying mechanisms that determine how these shifts affect species interactions are not always clear (Rafferty et al. 2013). Early arriving species often dominate over later-arriving species (i.e., priority effects) via several mechanisms, including resource pre-emption, habitat modification, or direct interference (Connell and Slatyer 1977). Such priority effects have been observed in many taxa, including plants (Kardol et al. 2013), fish (Almany 2003; Geange and Stier 2010), terrestrial invertebrates (Shorrocks and Bingley 1994), aquatic invertebrates (Louette and De Meester 2007; Rasmussen et al. 2014), and amphibians (Alford and Wilbur 1985; Hernandez and Chalcraft 2012). However, the underlying mechanistic processes of priority effects are largely unknown for many systems. Therefore, a greater understanding of the processes (e.g., physical interference or resource pre-emption) that determine the outcome of phenological variation on intraspecific and interspecific interactions may facilitate a robust understanding of the importance of phenological shifts on species interactions and community structure.

Species interactions may be altered by additional factors that either suppress or magnify the impacts of phenological variation. In particular, consequences of advancements or delays in the timing of breeding may be offset or augmented by variable individual or population growth rates resulting from differences in population densities (Hopper et al. 1996; Reed et al. 2015). Such synergistic interactions between density dependence and phenological shifts may be especially relevant for predator–prey interactions, whose outcomes are determined by body size (e.g., gape limitations), as intra- and interspecific density dependence and interspecific differences in phenology can both dictate body size differences. Shifts in interaction type or strength may, therefore, ensue through either density-dependent or phenology-dependent processes (Yang and Rudolf 2010), yet simultaneous tests of these effects on species interactions are rare (but see Sredl and Collins 1991; Hunter and Elkinton 2001; Durant et al. 2005; Stier et al. 2013; Reed et al. 2015).

We conducted a mesocosm experiment to test how shifts in phenology and larval densities influenced predation by ringed salamanders (*Ambystoma annulatum*) on coexisting spotted salamanders (*A. maculatum*). Amphibians

are good model system for these tests, because numerous studies on breeding phenology (Morin 1987; Boone et al. 2002; Orizaola et al. 2010; Rasmussen and Rudolf 2015), density-dependent competition (Wilbur 1972; Van Buskirk and Smith 1991; Scott 1994), and priority effects (Alford and Wilbur 1985; Wilbur and Alford 1985; Hernandez and Chalcraft 2012) provide a substantial baseline of information on how each process affects species interactions. Two emergent paradigms from this large body of work are: (1) asynchronous breeding between species can create body size asymmetries among larval stages, which can impact the type (e.g., competition and predation) and strength of species interactions; and (2) larval salamanders are gape-limited predators, and increased density dependence could offset priority effects advantages obtained by breeding earlier or further augment negative effects of delayed breeding.

We experimentally manipulated phenology of each species by introducing larvae to outdoor mesocosms at differing times that represented normal and delayed breeding, simultaneous to altering predator (ringed salamander) density. We hypothesized that phenological shifts would influence interactions through one of two potential predicted pathways: (1) phenological shifts that increase size disparity (e.g., early breeding of ringed salamanders and late breeding of spotted salamanders) would result in strong interspecific effects via increased predation relative to competition (Electronic Supplementary Material [ESM] 1) and (2) shifts that decrease size differences (e.g., ringed salamanders breeding later and spotted salamanders breeding earlier) will shift interactions from predation to solely competition (ESM 1). In all cases, we hypothesized that higher densities of ringed salamanders would result in both reduced intraspecific growth rates of the predator and size disparities between species, and further compound phenology effects (ESM 1). We also investigated the underlying mechanisms of priority effects by which ringed salamanders limit spotted salamanders (preemptive consumption of the shared resource or direct interactions [e.g., predation]), and expected that the latter process would be the dominant interaction. Finally, we tested whether shifts in phenology and variable densities would impact different trophic levels, with the expectation that higher densities of salamanders would have the largest impacts on zooplankton and phytoplankton biomass.

Methods

Study system

Ringed salamanders are endemic to the Ozark and Ouachita Mountains of Missouri, Arkansas, and Oklahoma, USA (Petranka 1998). Adults migrate to ponds in September–November to breed larvae overwinter in ponds and

undergo metamorphosis from late April–June (ESM 1; Semlitsch et al. 2014). Spotted salamanders are widely distributed across the eastern USA (Petranka 1998) and in Missouri breed in late February–early April and undergo metamorphosis from June to October (Semlitsch and Anderson 2016). The mean breeding date can vary by up to 28 days among years and ponds for each species (Semlitsch et al. 2014; Semlitsch and Anderson 2016). Thus, larvae of these two species co-occur in ponds anywhere from several weeks to months (Anderson and Semlitsch 2014; Anderson et al. 2015), resulting in variable sizes between species. Predation is primarily unidirectional (ringed salamanders eating spotted salamanders) because of the seasonal differences in breeding phenology. Larger ringed salamander larvae are also more voracious predators than smaller larvae on spotted salamander hatchlings (Anderson et al. 2016a), indicating that phenology and predator density, both determinants of interspecific larval size differences, have strong implications for their interactions. These species share substantial overlap in basal resources, similar to intraguild predation (Polis et al. 1989), though they do not use or share an exclusive basal resource.

Experimental setup

We conducted the experiment in 1000 l outdoor mesocosms (hereafter tanks) arranged in a rectangular array on the University of Missouri campus. We filled tanks with well water on 13 Sep 2013, and let them sit for 10 days to dechlorinate. We added 1.25 kg of dry leaves (primarily *Quercus spp.*, *Carya spp.*, and *Acer spp.*) that had been collected from Baskett Wildlife Research Area near Ashland, MO, and water (4 l) from nearby ponds to inoculate tanks with planktonic organisms. We sieved water samples through an aquarium net to remove any large predaceous invertebrates prior to addition. We initially covered tanks with mesh lids to prevent colonization by insects, but we removed them at the start of the experiment to facilitate colonization by prey (e.g., chironomids) and decrease the likelihood of freezing during winter months. Most aquatic predators that would colonize tanks (e.g., dragonflies) had stopped flying by this point, though one tank was colonized by predaceous larval stages of scavenging beetles (Hydrophilidae); omission or inclusion of this tank did not affect any of the results, so we kept it in the analysis.

We collected late-stage egg masses of ringed salamanders on 27 Sep 2013 from a permanent pond at Fort Leonard Wood, MO, and transported them to a greenhouse near the tank array. To minimize genetic bias of early vs late-breeding individuals on the outcomes of the experiment, we used only clutches from early breeding adults and spread individuals across our phenology treatments. To achieve this phenology manipulation, we cut each egg mass approximately

in half with scissors, and placed one half in a cold storage room (ca. 8 °C) and one half in a greenhouse (ca. 22 °C). Eggs in the greenhouse hatched within 48 h, whereas those in the cold room began hatching on 19 Oct and completed hatching within 12 days. Hatchlings were kept cold and fed a small aliquot of concentrated zooplankton 4 days prior to addition. We recognize that temperature regimes can influence hatchling traits such as body size and development (Orizaola et al. 2010), and we account for this difference in some of the metrics we analyzed (see below). Ultimately, this was a trade-off in balancing confounding genetic versus physiological effects, and our approach is commonly used for manipulating phenology (e.g., Nosaka et al. 2015; Rasmussen and Rudolf 2015; Murillo-Rincón et al. 2017).

We collected eggs of spotted salamanders on 05 Apr 2014 also from ponds at Fort Leonard Wood. Egg masses were cut in half and placed in the same rooms where ringed salamander eggs had been stored (8 °C for cold and 19 °C for warm). However, the eggs experienced some mortality in the greenhouse due to unanticipated temperature fluctuations, and had to be supplemented with additional egg masses that were not cut in half. Thus, our ringed salamander component had equivalent genetic contributions mixed across phenology treatments, but spotted salamanders were slightly confounded in genetic contribution. We do not expect this difference greatly biased our results though admit that it is a possibility.

Phenology–density experiment

This experiment consisted of a 4 × 2 design (phenology × ringed salamander density) using 32 tanks. Our phenology treatments included an “early” and “late” addition for each species to represent early- or late-hatching egg masses, resulting in four possible phenology combinations (read as ringed salamander–spotted salamander): early–early, early–late, late–early and late–late. In this context, the early treatments correspond to approximately the mean hatching date for each species, and the late treatments correspond to delayed hatching that approaches the tail end of their breeding distributions (Semlitsch et al. 2014; Semlitsch and Anderson 2016).

Each tank contained one density of spotted salamanders ($N = 24$), and one of two densities of ringed salamanders (low: $N = 8$, 3.5 per m²; high: $N = 24$, 10.9 per m²). The low densities we used match high natural densities of each species (mean ± SD, ringed: 1.8 ± 1.8 larvae per m²; spotted: 1.6 ± 2.6 larvae per m²; Ousterhout et al. 2015), permitting our high-density treatments to test for strong density-dependent effects. We had four replicates of each *Phenology–Density* treatment combination. We added ringed salamander hatchlings to tanks assigned the “early” phenology for both density treatments on 03 Oct 2013, and the

“late” treatments 31 days later on 03 Nov 2013. We added spotted salamander hatchlings to tanks assigned the “early” treatments on 18 Apr 2014, and the “late” treatment 21 days later on 09 May. Prior to addition, we photographed hatchlings over a ruler for a subset of hatchlings for each species in each phenology treatment (ringed: $N = 586$; spotted: $N = 739$). From these photos, we measured total length (TL) using ImageJ (Rasband 1997) to assess species differences and how rearing conditions impacted initial hatchling size. We captured a subset (3–5 individuals) of larvalringed salamanders from each tank during the second week of April, and measured SVL (defined as the tip the snout to the distal junction of the tail and hind limbs) using ImageJ to assess predator size at the time of prey addition. In the late April, we began checking all tanks for metamorphs (individuals with reabsorbed gills) at least every other night. We removed metamorphs, and recorded snout–vent length (SVL) and mass. We also determined larval period length, the number of elapsed days from the date of introduction. All tanks were drained 16 and 17 Jul 2014 and we carefully searched the leaf litter for the remaining salamanders.

Priority Effects experiment

In a second experiment, we tested the mechanism by which the prior establishment of ringed salamanders affected spotted salamanders: resource pre-emption or interference/predation. We set up all tanks for this experiment in an identical manner as above and interspersed them within the *Phenology–Density* experimental array. We used a 2×2 full factorial design for priority effect treatments: two priority effects (sequential and synchronous, described below) and two predator density treatments (low: $N = 8$; high: $N = 24$) with three replicates of each treatment. In the sequential treatment, ringed salamander larvae were added on 03 Oct 2013 at either low or high density, and then removed prior to the addition of spotted salamanders ($N = 24$) on 27 Apr 2014; this treatment represents the situation, where ringed salamanders metamorphose prior to hatching of spotted salamanders in the spring. For the synchronous treatment, both species were added at the same time on 27 Apr 2014 to tanks that had been set up the previous fall but left devoid of salamanders (see below for ringed salamander details). This test isolates the effects of the previous resource depletion from other interactions (concurrent exploitative or interference competition and predation) because larvalringed salamanders did not have time to consume zooplankton prior to adding spotted salamanders (i.e., the sequential treatment). We admit this design did not permit us to directly monitor predation, our expectation for the dominant interaction in the synchronous treatment. However, spotted salamanders typically have higher survival in tanks in the absence of ringed salamanders predators (Anderson and Semlitsch

2014, 2016), suggesting that predation was a more likely process. We also set up two control treatments, where we added either 24 or 48 hatchling spotted salamanders to tanks on 27 Apr, which served as controls against the minimum and maximum salamander densities.

On 21 Apr 2014, we began capturing ringed salamander larvae from tanks in the sequential treatment with aquarium nets and collapsible mesh minnow traps. This process continued for 6 days, at which point we did not observe or capture any more ringed salamander larvae. No remaining ringed salamanders were captured at the end of the experiment in the sequential treatments, indicating that all larvae had been successfully removed prior to the addition of spotted salamanders. Sequential treatment tanks had been assigned a matching tank within the synchronous treatment: ringed salamander larvae removed from the former were transferred to the latter after capture. Prior to this move, larvae were dorsally photographed over a ruler to measure SVL using ImageJ. For the low- and high-density control treatments, we added either 24 or 48 hatchling spotted salamanders on 27 Apr 2014.

Community sampling

We sampled all tanks in both experiments three times to assess phytoplankton and zooplankton biomass (09 Nov 2013, 09 Apr 2014, and 09 May 2014). These dates correspond approximately to when we added lateringed salamanders, early spotted salamanders, and latespotted salamanders, respectively. We used the standard methods for sampling each trophic level (detailed in ESM 2).

Analyses

All analyses were conducted using R v3.3.0 (R Core Team 2016). We first tested whether hatching TL varied between species, phenology treatment, and their interaction using ANOVA. For both the *Phenology–Density* and *Priority Effects* experiments, we generated mean values for each tank (our experimental unit) for the following metrics: larval SVL (ringed salamanders only), metamorph SVL, relative growth rate (RGR), and larval period length. Snout–vent length, TL, and mass at metamorphosis were all highly correlated ($r > 0.85$) and resulted in similar conclusions, so we only report SVL. Relative growth rate was calculated as $[\ln(\text{SVL}_{\text{metamorph}}) - \ln(\text{TL}_{\text{hatchling}})] \cdot \text{days}^{-1}$, and provides a test of treatments effects while accounting for differences in the initial hatchling size among phenology treatments. We initially analyzed all responses using MANOVA with phenology, density, and their interaction as factors, which resulted in a significant interaction term of phenology and density for ringed salamanders ($P = 0.002$), and significant effects of phenology and

density for spotted salamanders (both phenology and density, $P < 0.001$). For the *Phenology–Density* experiment, we then analyzed each response using two-way ANOVAs, with the main effects of density, phenology treatment, and their interaction. We also analyzed survival of each species using generalized linear models with a quasi-binomial distribution (logit link), which better corrected overdispersion than using an individual-level random effect. We calculated survival as the total number of larval (20% of all individuals were still larvae for *A. maculatum* at the conclusion of the experiment) and metamorphosed individuals at the end of the experiment, as remaining larval individuals were typically large enough to complete metamorphosis. We again used phenology, density, and their interaction as predictor variables. Because we did not initially block the experiment, we tested whether individual rows of the tank array affected our results, but this factor was not significant and thus removed from further analysis. We removed non-significant interaction terms when present and tested for the main effects of each predictor; phenology and density were always retained in each model. We also computed adjusted R^2 values for SVL, RGR, and larval period length models and McFadden R^2 for the survival model.

For the *Priority Effects* experiment, we analyzed the same metrics (larval and metamorph SVL, RGR, larval period length, and survival) and used the same model error structures as the *Phenology–Density* experiment. For ringed salamanders, the only predictor variable was their initial density. For spotted salamanders, we tested for differences in each response across the two control conditions and the four experimental treatments. We also separately examined whether the initial density of ringed salamanders influenced metrics of spotted salamander metamorphs in the synchronous and sequential treatments, where they interacted either directly or indirectly, respectively. We report similar R^2 metrics as above.

For the community sampling, we analyzed chlorophyll *a* (chl *a*), a proxy for phytoplankton biomass, and the biomass of the two most dominant groups of zooplankton, *Daphnia* and adult copepods (primarily Cyclopoida) using linear mixed models in the ‘lme4’ package (Bates et al. 2015). We $\log(x + 1)$ -transformed each biomass estimate, and included sample date and mesocosm as random effects to account for the repeated sampling of tanks. We tested for significance of phenology and initial density using Kenward–Rogers approximate F tests in the ‘car’ package (Fox and Weisberg 2011). We also report marginal and conditional R^2 values (R_m^2 and R_c^2 , respectively), which correspond to the amount of variation explained by the fixed and random effects, respectively (Nakagawa et al. 2013). Below, we report the P values and model R^2 , but all test statistics, including other effect size measures, (η^2) are in ESM 3.

Results

Hatchling size at the time of addition varied significantly by an interaction of phenology treatment and species ($P < 0.001$; adj. $R^2 = 0.65$). Post hoc Tukey contrasts showed that all species–phenology combinations were significantly different from one another. Within a species, ringed salamander hatchlings were on average 4.5 mm longer and spotted salamander hatchlings were 1.0 mm longer in the late phenology compared to the early phenology treatment (Fig. 1a). For between species comparison, ringed salamanders were on average 1.0 mm shorter than spotted salamanders in the early phenology but 2.5 mm longer in the late phenology.

Phenology–Density

The interaction of phenology treatment and initial density was not significant for larval SVL of ringed salamanders at the time of the early spotted salamander addition ($P = 0.80$; Fig. 1b). There were significant effects of phenology and density on larval SVL (phenology: $P < 0.001$; density: $P = 0.02$; $R^2 = 0.64$). Larvae from low-density treatments were on average 2.1 mm larger than high-density treatments, and larvae from early treatments (early–early and early–late) were approximately 6 mm larger than larvae from the late treatments (late–early and late–late; Fig. 1b).

The interaction of phenology treatment and initial density was not significant for SVL, larval period length, or RGR of ringed salamander metamorphs (all $P > 0.08$). Metamorphs were significantly greater in SVL, on average 5 mm longer, when reared at low compared to high densities ($P < 0.001$; $R^2 = 0.54$; Fig. 2a), but phenology treatment effects were not significant ($P = 0.12$). Differences in RGR were significant for each of phenology and density treatments (phenology: $P < 0.001$; density: $P < 0.001$; $R^2 = 0.76$); RGRs were 24% higher in the early–early and early–late treatments compared with the late–early and late–late treatments, and 15% higher at low densities compared to high initial densities (Fig. 2c). Initial density and phenology treatments were each significant predictors of ringed salamander larval period length (density: $P = 0.003$; phenology: $P < 0.001$; $R^2 = 0.90$); larval periods were on average 27 days longer in the early–early and early–late treatments compared with the late–early and late–late treatments, and 5 days longer in high-density compared to low-density treatments (Fig. 2e). A significant interaction of phenology and initial density predicted survival of ringed salamanders ($P = 0.002$; McFadden $R^2 = 0.63$). Post hoc Tukey contrasts showed that at high initial densities, survival was 40 and 50% lower in the early–early treatment compared to the late–early and late–late treatments, respectively (Fig. 2g). The low-density early–late treatment was

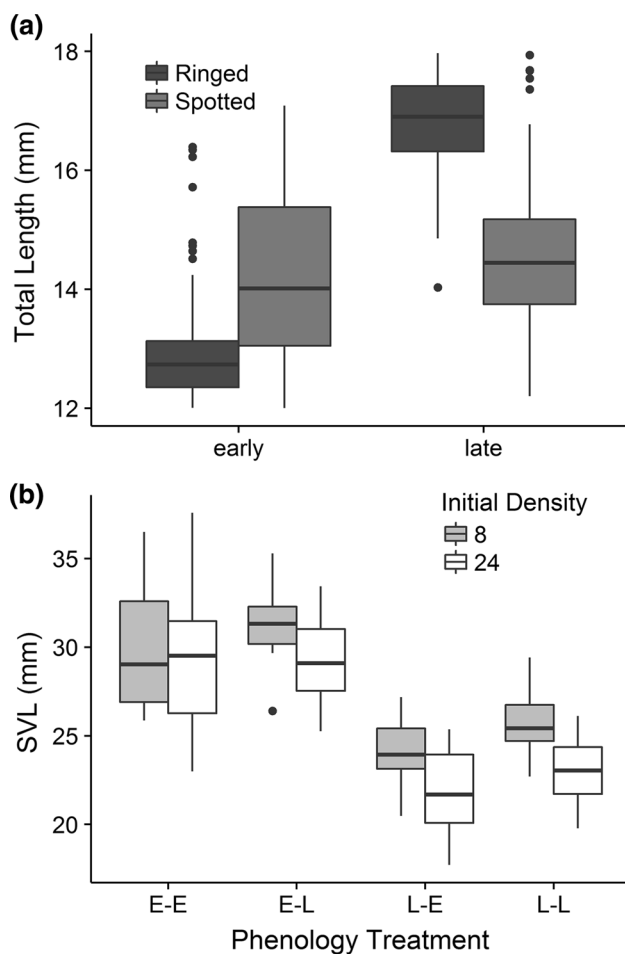


Fig. 1 **a** Hatching total length of ringed (*Ambystoma annulatum*; darker boxes) and spotted (*A. maculatum*; lighter boxes) salamanders at the time they were added to tanks. Early and late correspond to 3 Oct 2013 and 3 Nov 2013 for ringed salamanders, respectively, and 18 Apr 2014 and 9 May 2014 for spotted salamanders, respectively. **b** Larval snout–vent length in April of ringed salamanders (*Ambystoma annulatum*) in the Phenology–Density experiment. The timing of measurement corresponded with approximately when spotted salamanders were added to tanks and when the second zooplankton sample was taken. Gray boxes are low-ringed salamander density ($N = 8$) and white boxes are high-ringed salamander density ($N = 24$). The x-axis labels correspond to the phenology treatments, read as ringed salamander–spotted salamander: early–early (E–E), early–late (E–L), late–early (L–E), and late–late (L–L)

12–19% higher than the other three low-density phenology treatments.

For spotted salamanders, the interaction of phenology and ringed salamander density was not significant for metamorph SVL, RGR, or survival (all $P > 0.18$; Fig. 2). For SVL, the effect of initial ringed salamander density was significant ($P = 0.002$, $R^2 = 0.31$; Fig. 2b), but phenology had no significant effect ($P = 0.12$). Metamorphs were on average 1.5 mm larger in the high-density compared to the low-density treatments. Relative growth rates of spotted

salamanders were significantly different between both ringed salamander density and phenology treatments (density: $P = 0.008$; phenology: $P = 0.03$; $R^2 = 0.37$; Fig. 2d). Metamorphs grew 8% faster at lowringed salamander densities compared with highringed salamander densities, and 15% slower in the late–late phenology treatment compared with the early–early treatment. Larval period length was predicted by a significant interaction of phenology and ringed salamander density treatments ($P = 0.01$; $R^2 = 0.63$; Fig. 2f). In general, metamorphs in the late–late highringed salamander density treatment took the longest to metamorphose among other high-density treatments, and compared to the low-density late–late treatment. Survival was significantly affected by ringed salamander density ($P = 0.006$; McFadden $R^2 = 0.25$; Fig. 2h), but phenology treatment had no effect. Survival was on average 23% higher at low densities compared with high densities. Survival and SVL were also negatively correlated ($r = -0.57$, $P = 0.001$).

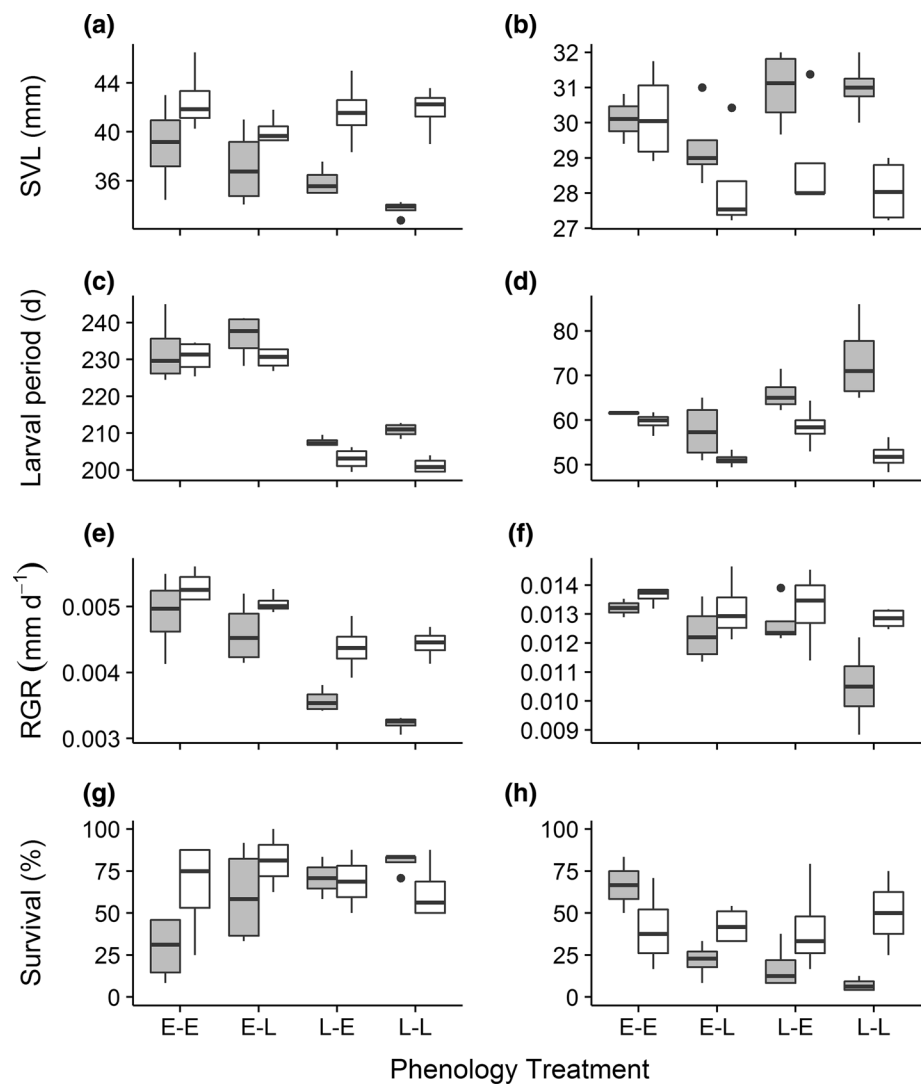
Chl *a* tended to be lower and *Daphnia* biomass higher in low-density treatments (ESM 3). However, only *Daphnia* biomass was significantly different between initial density treatments ($P = 0.009$), and phenology had no significant effects for either response (chl *a*: $R_m^2 = 0.02$, $R_c^2 = 0.35$; *Daphnia*: $R_m^2 = 0.12$, $R_c^2 = 0.20$). Neither treatment significantly affected copepod biomass (both $P > 0.8$; $R_m^2 = 0.004$, $R_c^2 = 0.93$).

Priority effects

Larvalringed salamanders averaged 30 mm SVL (range 23–42 mm) in the sequential treatments at the time they were moved to synchronous treatments, and were on average 5 mm larger at low compared to high densities, though the difference was not statistically significant ($P = 0.26$; $R^2 = 0.09$). This general trend continued for metamorphs, where individuals in low-density treatments were on average 3 mm longer in SVL, had higher relative growth rates, and shorter larval periods than metamorphs from high-density treatments, but the effects were not statistically significant (all $P > 0.30$; all adj. $R^2 < 0.02$; ESM 3). Survival did not vary by density treatment ($P = 0.47$).

Snout–vent length, RGR, and survival of spotted salamander metamorphs all varied significantly among priority effect treatments (SVL: $P = 0.004$, $R^2 = 0.44$; RGR: $P = 0.02$, $R^2 = 0.33$; survival: $P = 0.002$, McFadden $R^2 = 0.50$). Larval period length was not significantly affected ($P = 0.55$; Fig. 3). Density and the interaction of density with priority effect treatments was also not significantly different for any response variable ($P > 0.28$). Metamorphs from the synchronous treatment were on average 3 mm larger than individuals from either control or the sequential treatments, and had higher growth rates in the synchronous treatment (Fig. 3). Survival of spotted

Fig. 2 Snout–vent length (SVL), relative growth rate (RGR), larval period length, and survival of ringed (*Ambystoma annulatum*, left column) and spotted (*A. maculatum*, right column) salamanders in relation with phenology and initial density treatments in the Phenology–Density experiment. Gray boxes are low-ringed salamander density ($N = 8$) and white boxes are high-ringed salamander density ($N = 24$). The x-axis labels correspond to the phenology treatments, read as ringed salamander–spotted salamander: early–early (E–E), early–late (E–L), late–early (L–E), and late–late (L–L). Note the different vertical-axis ranges between species



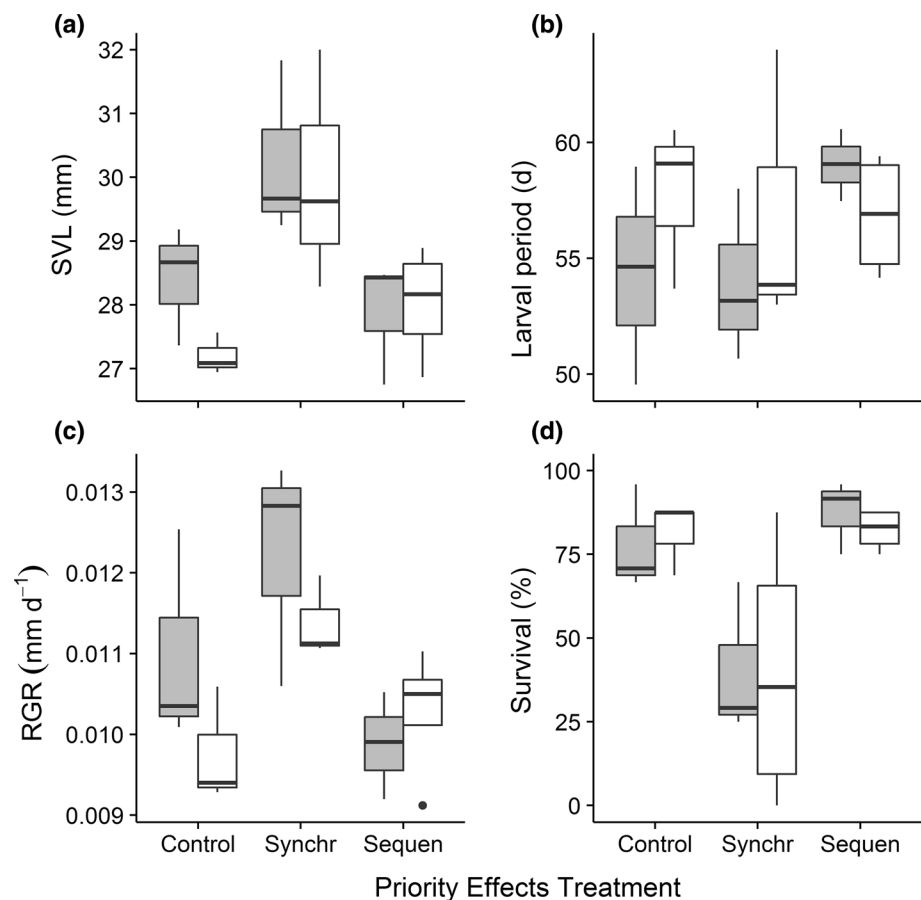
salamanders was 39 and 33% higher in the sequential and control treatments compared with the synchronous treatment, respectively (Fig. 3).

For trophic effects in the *Priority Effects* experiment, chl *a* biomass was significantly affected by both priority effects and density treatments (priority effects: $P = 0.002$; density: $P = 0.005$; $R_m^2 = 0.29$, $R_c^2 = 0.34$; ESM 1). Chl *a* was lower in low-density compared with high-density treatments, and highest in the sequential treatment. Priority effects treatments were marginally significant for *Daphnia* biomass ($P = 0.06$) and density was not significant ($P = 0.65$; $R_m^2 = 0.13$, $R_c^2 = 0.35$). *Daphnia* biomass was highest in the synchronous treatment and lowest in the sequential treatment. Copepod biomass was not significantly affected by either density ($P = 0.08$) or priority effects treatments ($P = 0.98$; $R_m^2 = 0.04$, $R_c^2 = 0.83$).

Discussion

Phenological variation and density dependence are two factors that commonly influence body size differences among individuals within and among species, which can affect intra- and interspecific interactions (Yang and Rudolf 2010; Miller and Rudolf 2011). However, the synergistic effects of phenology and density on species interactions have rarely been investigated (Hopper et al. 1996; Hunter and Elkin-ton 2001; Stier et al. 2013; Rasmussen and Rudolf 2015; Reed et al. 2015). For most response variables, we found that predator phenology and initial density had either singular or additive effects on the predator or prey, but that density effects were more pronounced for the prey. Only predator survival and prey larval period length were affected by synergies between phenology and density. We also found

Fig. 3 Snout–vent length (SVL), relative growth rate (RGR), larval period length, and survival of spotted salamanders (*Ambystoma maculatum*) in the *Priority Effects* experiment. In the sequential (‘Sequen’) and synchronous (‘Synchr’) treatments, *gray boxes* are low-ringed salamander density ($N = 8$) and *white boxes* are high-ringed salamander density ($N = 24$). In the control treatments, the *gray boxes* are low ($N = 24$) and *white boxes* are high ($N = 48$) spotted salamander density, to control for spotted salamander density and overall density, respectively



indirect support for predation as the likely mechanism by which the predator in our system limits its prey, as opposed to resource pre-emption. Finally, predator phenology and density had limited impacts on trophic cascades. Overall, our study provides critical insight into the relative magnitude of phenological variation needed to affect species interactions compared with other processes (e.g., density dependence), and further such inquiries may help resolve the importance of phenological shifts on species interactions, especially those subject to change under future climate scenarios.

Phenology and density

Predator density and phenology had highly variable effects on traits of the predator (ringed salamanders). Snout–vent length was only affected by density, but RGR and larval period length were influenced by additive effects of both factors, and survival was affected by synergies between them. Our results are consistent with other demonstrations of density-dependent competition (Wissinger 1989; Van Buskirk and Smith 1991), where growth rates and other individual traits were positively influenced in low-density environments. The reason for synergistic effects of phenology and density on ringed salamander survival is a bit unclear for

the early–early high-density treatment, as manipulated and environmental variables (e.g., temperature) were not outside normal conditions experienced by this species. However, the absence of an interaction for SVL and RGR is also notable, because it indicates different combinations of phenology and densities may be equivalent in how they affect individual traits (e.g., metamorph SVL in the low-density late treatments were not different from the high-density early phenology treatments). As body size at metamorphosis is generally a good predictor of adult fitness for amphibians that metamorphose close to maturation size (Semlitsch et al. 1988; Altwegg and Reyer 2003; Earl and Whiteman 2015), as is the case in our focal species, understanding the conditions that influence body size is critical to understanding selective pressures on individuals that would lead to altered population dynamics.

We observed strong compensatory growth in the predator, where the late additions of ringed salamanders overcame a 30-day deficit in breeding phenology to metamorphose at the same time as the early additions. At high densities, such growth occurred at a cost of reduced body size at metamorphosis. Compensatory growth has been documented in numerous taxa (Metcalf and Monaghan 2001), but especially in organisms that inhabit ephemeral aquatic

ecosystems, as such plasticity is likely critical to advance development rates and complete metamorphosis under deteriorating habitat conditions (Altwegg 2002; Stoks et al. 2006; Orizaola et al. 2010, 2014). Such compensatory growth in ringed salamanders is somewhat surprising, however, because their long larval period requires them to inhabit more permanent ponds, suggesting reduced selection from pond drying on growth rates for this species.

Predator density had the strongest effect on nearly all traits of our prey species, the spotted salamander. We observed that spotted salamanders were larger at metamorphosis and their survival was lower at high predator densities (Anderson and Semlitsch 2014). The correlation of these traits stems from reduced competition among the surviving prey, or thinning effects (Van Buskirk and Yurewicz 1998; Brodin and Johansson 2002), which permits higher growth rates of individuals once they exceed gape limits of the predator. Phenological variation only affected larval development in spotted salamanders, primarily through lengthening of the larval period when hatchlings were added late and at a high density. Such a scenario may have important implications if hydroperiod length is a limiting factor; in ephemeral pools, larvae may have difficulty achieving the minimum size for metamorphosis when faced with both increased competition (density) and less time to metamorphose due to later breeding.

Asymmetric effects of altered phenology on traits of interacting species may be a common phenomenon, and appear to disproportionately affect prey more than predators (Sredl and Collins 1991; Brundage et al. 2014; Nosaka et al. 2015; Rasmussen and Rudolf 2016), though tests that consider simultaneous shifts in predators and prey are relatively rare. We observed the opposite result; predator density primarily affected the prey, whereas the predator was affected by a combination of phenology and density in varying strengths, depending on the response. This departure from the previous studies could indicate that the timescale of phenology is critical towards explaining when phenological variation is important: shifts may not affect interactions between species with greater temporal separation in ontogenies as much as shifts between species that have more synchronous ontogenies. For example, several studies found even modest phenological shifts affected species interactions of taxa that breed in the same season (Rasmussen et al. 2014; Rasmussen and Rudolf 2016). In our study, 20–30-day phenological shifts represented realistic variation in breeding phenology, but were not enough to substantially influence body size differences between species; larvalringed salamanders were still large enough to consume spotted salamander hatchlings in all treatments (Anderson et al. 2016a). Our experiment indicates that, at least in our system, extreme density dependence within the predator/prey or substantial phenological shifts would be necessary to affect size asymmetries enough for a

switch of interaction type (e.g., predation to competition) to occur in this system (Yang and Rudolf 2010). With certain simplifying assumptions about larval growth patterns (ESM 4), ringed salamander breeding phenology would have to undergo additional shifts of ca. 33 day beyond our late treatment at high densities (equivalent to 06 Dec), and 45 day at low densities (18 Dec) to cause a switch in interaction type; the total number of days beyond the mean breeding date this simple model explored (63–75 days) corresponds to realistic shifts reported in other taxa, including amphibians (Parmesan 2006; Todd et al. 2011). However, more modest variation in density and phenology, in combination with other processes that similarly limit body size (e.g., temperature; Indermaur et al. 2010), may ultimately result in switches in interaction type (e.g., predation to competition; Yang and Rudolf 2010). Indeed, larvalringed salamander sizes at the time of spotted salamander breeding in natural populations vary more widely compared to the sizes observed in this experiment (Ousterhout et al. 2015; Anderson et al. 2016b), which could be the byproduct of these multiple stressors.

We compared phenological shifts in breeding between two dates for each species, analogous to shifts in the mean phenology. However, other types of phenological shifts, such as altered variance, skewness, or earliest/last dates, may be more critical to species interactions (CaraDonna et al. 2014; Rasmussen and Rudolf 2015, 2016). We expect that altered variance in breeding would be particularly important in the development of size-structured populations and communities: a greater number of breeding pulses spread out across a longer time period may increase size variance both within and between species (Rasmussen et al. 2014; Murillo-Rincón et al. 2017), though predation could simultaneously decrease size variance if subsequent cohorts are eliminated. Alternatively, decreased phenological variance (i.e., greater synchrony) may reduce size structure but increase density-dependence, which we found to be a strong predictor of both predator and prey responses. Further tests are, therefore, needed to determine what temporal component of phenological variation, if any, is most critical towards explaining shifts in species interactions, and if certain aspects of phenological change would be mollified by other processes such as density dependence.

Priority effects

The mechanisms by which early colonizing individuals either enhance or limit subsequent arrival patterns has been a long-standing area of investigation in ecology, and likely have important consequences for interactions altered by phenology. However, tests of which mechanism is pervasive are rare. One of the strongest examples also occurred in pond communities, where Hernandez and Chalcraft (2012) found that resource depletion by overwintering anuran tadpoles

was the dominant effect on spring anuran tadpoles, with ensuing changes to interaction strengths between subsequent cohorts. In contrast to this result, we found that prior occupancy of tanks by ringed salamanders with no physical interactions did not influence body size or survival of spotted salamanders, resulting in similar patterns to control treatments without ringed salamanders. However, when the two species co-occurred without prior resource depletion present, spotted salamander survival was greatly reduced, indicating that the relative impacts of resource depletion on spring-breeding species are substantially less than more direct effects. We cannot entirely disentangle the exact process (avoidance mechanisms of the prey, interference competition by the predator, or predation), but we speculate predation as the likely culprit due to high foraging rates by ringed salamanders on spotted salamanders in laboratory studies (Anderson et al. 2016a) and because competition alone rarely results in variable mortality within mesocosms for these species (Anderson and Whiteman 2015; Anderson and Semlitsch 2016; Ousterhout and Semlitsch 2016). Behavioral avoidance seems unlikely to have occurred as spotted salamanders do not always respond to predatory threats by congeners (Walls 1995). Further identification of priority effects mechanisms is critical in systems where phenology is changing, as it permits insight into how interactions may subsequently shift.

Community effects

Phenological shifts have been predicted to affect multiple trophic levels in simulation studies (Nakazawa and Doi 2012; Revilla et al. 2014), and from some observational studies (Durant et al. 2007; Both et al. 2009). However, empirical tests of such effects are rarer (Both et al. 2009). We observed no effect of phenology and only minimal effects of density on lower trophic levels. We mainly found reduced *Daphnia* biomass with increasing salamander density in the *Phenology–Density* experiment, and weaker positive effects of density on phytoplankton biomass in the *Priority Effects* experiment. Other studies have shown top predators can alter the composition and abundance of lower trophic levels via trophic cascades (Pace et al. 1999), including pond ecosystems (Holomuzki et al. 1994; Blaustein et al. 1996; Eitam et al. 2005; Urban 2013), which is weakly corroborated by our results. This reduced effect could be due to the highly stochastic dynamics of plankton in pond ecosystems, and our three sampling points were not enough to capture treatment effects. Recent findings by Rowland et al. (2017) support this idea, which showed the strength of top–down control of pond food webs by salamanders changed temporally. Our density treatments may also have not been insufficient to produce a measurable impact on lower trophic levels,

even though they were at or above natural densities. Nevertheless, we expect that further examination of phenological shifts propagating through a community could be a promising area of future research.

Conclusions

Experimental investigations of variation in phenology can set a baseline for understanding how phenology affects interspecific interactions, as well as simulate scenarios of how future phenological shifts will alter community structure under climate change (Visser and Both 2005; Forrest 2015). Such investigations, coupled with natural observations or modeling, would be exceedingly powerful to unravel the mechanistic pathways in species interactions associated with phenological shifts (Rafferty et al. 2013; Rasmussen et al. 2014). Documenting these asymmetric responses is important, because such findings may lead to greater insight into how species interactions are affected by phenological shifts occurring due to climate change. Not all species are changing in a similar manner, and thus, only certain interactions (or partners within interactions) may be influenced (Rafferty and Ives 2011; CaraDonna et al. 2014). It is also important to not discount alternative processes, such as density dependence, that may be equally or more important for determining the outcome of species interactions. Phenology and density may also respond to different environmental cues, leading to contrasting effects on population dynamics (Ficetola and Maiorano 2016). Monitoring density or other factors simultaneous to phenological variation may, therefore, elicit a better understanding of when phenological variation becomes important for species interactions, and could be critical elements to include in long-term monitoring of phenology. Assessments of these and other synergistic effects are an important next step in understanding how phenological variation will alter species interactions and food webs.

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Authors contributions TLA and RDS designed the study, TLA and FER performed the study, FER performed laboratory analysis, TLA analyzed data and wrote the manuscript, and TLA and FER edited the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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